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PEREGRINE FALCON PREDATION ON DUNLINS AND DUCKS AND KLEPTOPARASITIC INTERFERENCE FROM BALD EAGLES WINTERING AT BOUNDARY BAY, BRITISH COLUMBIA

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ABSTRACT.—At Boundary Bay, British Columbia, wintering Peregrine Falcons (*Falco peregrinus*) captured 94 Dunlins (*Calidris alpina*) in 652 hunts. The major hunting techniques were open attacks on flying flocks (62%) and stealth attacks on feeding or roosting flocks (35%). Success rates for these techniques were 9.1% and 23.6%, respectively. Sixty-five Dunlins were taken directly from the edge of flocks; 29 Dunlins were seized after they had split off from flocks or were flying alone. Adult peregrines were significantly more successful than immatures (26.8% vs. 9.0%). Peregrines captured one Green-winged Teal (*Anas crecca*) and three larger ducks. The teal was carried away, but the larger ducks were pirated by Bald Eagles (*Haliaeetus leucocephalus*). Eagles often joined peregrines that were chasing Dunlins; six eagles succeeded in either capturing the Dunlin or forcing a peregrine to drop its just-caught prey. It is postulated that peregrines wintering at Boundary Bay avoid prey species that are too heavy to be carried out of reach of kleptoparasitic eagles. Female peregrines aggressively chased off other females, but they tolerated males. Females often joined males that were chasing Dunlins; 14 males were forced to surrender their prey to females. Four peregrines pirated Dunlins from Merlins (*Falco columbarius*).

KEY WORDS: *Bald Eagle*, *Haliaeetus leucocephalus*; *Dunlin*; *Calidris alpina*; *Peregrine Falcon*; *Falco peregrinus*; *British Columbia coast*; *ducks*; *hunting habits*; *kleptoparasitism*.

PREDACIÓN DEL HALCÓN PEREGRINO SOBRE CHORLITOS Y PATOS, E INTERFERENCIA KLEPTOPARASITICA DEL AGUILA CALVA TEMPERANDO EN LA BAHIA DE BOUNDARY, BRITISH COLUMBIA

RESUMEN.—En sitios de destinacion final de la migración de otoño, el halcón peregrino (*Falco peregrinus*) capturó 94 chorlitos (*Calidris alpina*) en 652 cacerías/persecuciones, en la Bahía de Boundary, British Columbia. Las técnicas de cacería más sobresalientes fueron ataques abiertos sobre parvadas al vuelo (62%) y ataques furtivos sobre parvadas forrajeando o perchando (35%). Las tasas de éxito para esta técnicas fueron 9.1% y 23.6%, respectivamente. Sesenta y cinco chorlos fueron tomados directamente del borde de la bandada; 29 chorlitos fueron atrapados después de haberse separado de la bandada o estaban volando solos. Los peregrinos adultos fueron significativamente más exitosos que los inmaduros (26.8% vs. 9.0%). Los peregrinos capturaron un pato aliverde (*Anas crecca*) y tres patos más grandes. El pato aliverde fue llevado/apartado, pero el pato grande fue robado por aguilas calvas (*Haliaeetus leucocephalus*). Las águilas a menudo se unen a los peregrinos que están persiguiendo chorlitos; seis águilas tuvieron éxito, ya sea capturando chorlitos o forzando a los peregrinos a soltar su recién atrapada presa. Se ha postulado que los peregrinos que temperan en la Bahía de Boundary evitan especies de presas que son demasiado pesadas para ser llevadas fuera del alcance de águilas kleptoparasíticas. Las hembras de peregrino persiguen agresivamente otras hembras, pero toleran a los machos. Las hembras a menudo se unieron a los machos que estaban cazando chorlitos; 14 machos fueron forzados a ceder su presa a las hembras. Cuatro peregrinos robaron los chorlitos a los esmerejones (*Falco columbarius*).

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In their nearly worldwide range, Peregrine Falcons (*Falco peregrinus*) prey on a wide variety of birds, although they may locally specialize on very few species (Brown and Amadon 1968, Palmer 1988). The size of the prey taken is partly determined by the sex of the peregrine because females are about one-third heavier than males. This sexual size-dimorphism has spawned several hypotheses, including that it widens the range of prey that can be taken by paired falcons (Selander 1966, Cade 1982). Although both sexes of peregrines may hunt the same prey species, such as the Rock Dove (*Columba livia*) in human-altered ecosystems (Ratcliffe 1993, Frank 1994), or murrelets (*Brachyramphus* spp.) over the ocean (Beebe 1960, Dekker and Bogaert 1997), in many habitats female peregrines tend to kill larger prey than do males. For example, in central Alberta, migrant female peregrines predominantly killed ducks (Anatidae), while the males took sandpipers (Scolopacidae) and small passerines (Dekker 1980, 1988). Peregrines wintering in coastal agricultural regions of British Columbia and Washington also partitioned the food resource by gender (Anderson and DeBruyn 1979, Dekker 1987, 1995, 1999).

In the estuaries of western North America, a common prey of wintering peregrines is the Dunlin (*Calidris alpina*). Based on the remains of Dunlins killed by falcons, researchers in Washington and California reported that the majority are juveniles, which might be related to age-related flocking behavior (Kus et al. 1984, Warnock 1994). This paper details the hunting methods of both sexes of peregrines attacking flocks of Dunlins. It also reports on the duck hunting habits of these peregrines with particular reference to kleptoparasitic interference from Bald Eagles (*Haliaeetus leucocephalus*).

STUDY AREA AND METHODS

The study area is at Boundary Bay, which is part of the Fraser River delta (49°05'N, 123°00'W) in southwestern British Columbia. The bay is 16 km across and the intertidal zone is roughly 4 km wide at the lowest ebb. The tidal mud flats are bordered by a narrow strip of salt-marsh and a dyke that protects low-lying agricultural fields inland. Boundary Bay is a major stop-over for migratory waterbirds and a wintering refuge for ca. 20 000 ducks and 50 000 Dunlins. The only other shorebird to winter in the bay in some numbers (ca. 1000) is the Black-bellied Plover (*Pluvialis squatarola*) (Butler 1994, Butler and Kaiser 1995). Bald Eagles are common year-round and increase locally to 50–150 during January–February (Dekker 1999). For a more detailed description

of the Fraser delta and its avifauna, see Butler and Campbell (1987).

Between early November and early February, 1994–2003, I spent part or all of 151 d in the study area for a total of 940 hr. I walked the dyke or, especially during rain and strong winds, sat in a parked vehicle at a vantage point from where the tide flats were visible. To study the interaction of peregrines and their prey species, I used three principal methods: (1) flocks of ducks and shorebirds were monitored for alarm behavior such as sudden flushing; (2) the area was frequently scanned through binoculars to spot flying peregrines; and (3) perched peregrines were observed for varying lengths of time in the hope of seeing them hunt.

Peregrines were classified as either adult or immature, based on dorsal color and ventral markings (Palmer 1988). Males and females could only be separated with certainty, respectively, at the lower or higher end of their size range, because recorded weights of the heaviest male peregrines overlap with those of the lightest females, particularly between the subspecies occurring in western North America (Brown and Amadon 1968, White et al. 2002). Some falcons appeared typical of *F. p. pealei* (Beebe 1960), others of *F. p. anatum* (Palmer 1988). There is no evidence that peregrines of arctic origin (*F. p. tundrius*) winter in the bay. Already by the second week of February sightings of peregrines dropped off sharply, perhaps indicative of a return to breeding sites in the region.

Data were recorded in diary form and entered into an annotated table of hunts and kills. The term “hunt” is defined as a completed attack of which the outcome was known (Dekker 1980, 1988). A hunt could include one or more passes or stoops at the same Dunlin or flock. An attack on a flock and subsequent pursuit of a single Dunlin fleeing that flock were counted as one hunt. However, if the peregrine abandoned the pursuit and presently made another attack on the same or a different flock, this was counted as a second hunt. This definition of a hunt is equivalent to the term “attack” used by Cresswell (1996), but differs from “hunting flight” as formulated by Buchanan et al. (1986) and Buchanan (1996). Whether or not a hunt resulted in a kill was not always immediately apparent, especially at distances of >1 km. If the falcon ended a hunt by flying away fast and attacking other birds, without having been chased by a kleptoparasite, the preceding hunt was unsuccessful. On the other hand, if the falcon briefly slowed down with lowered feet, or if it retrieved something from the ground or water, then headed directly to shore, it was probable that prey had been caught. Supporting clues were pursuit by conspecifics, eagles or large gulls (*Larus* spp.). However, all probable captures were deleted from the data base unless they could be confirmed; for instance, by feeding activity. Perched peregrines were viewed through a 20–60 power telescope. Separate success rates were computed for adults and immatures and for the major strategies. Hunting data collected in 1994–98, which were presented in an earlier paper (Dekker 1998), were analyzed further and added to the data obtained in 2000–03. Data sets were compared statistically by G-test of independence (Sokal and Rohlf 1969).

Table 1. Success rates of various strategies used by Peregrine Falcons hunting Dunlins at Boundary Bay, British Columbia.

METHOD	HUNTS	KILLS	% SUCCESS
Stealth hunts	229	54	23.6
Open hunts	406	37	9.1
Unknown method	17	3	17.6
Totals	652	94	14.4

RESULTS

Dunlin Hunts. In hunting Dunlins, peregrines used two main methods: a low stealth attack on resting or feeding flocks, or an open attack on flying flocks. The stealth approach was used in 35% of hunts and resulted in 57% of total kills. The success rate of stealth hunts was significantly higher ($G = 17.53$, $P < 0.0001$) than open hunts (Table 1). Low stealth attacks were launched from perches or flapping flight, rarely by a stoop from high soaring flight. The Dunlins usually flushed at the very last moment and the peregrine might immediately

succeed in seizing its prey. Often one or more Dunlins dodged the falcon by dropping back onto the mud or water. Most took off at once with the peregrine occasionally pursuing them again. Others failed to rise and appeared to have been hit by the falcon. These prey, either crippled or dead, were retrieved in an unhurried pass by the peregrine.

In 62% of hunts, the falcons attacked Dunlins that had flushed well ahead or that were already airborne over the mudflats or ocean. If the approaching peregrine flew >10 m high, the Dunlins formed dense, globular flocks over the ocean. (See Buchanan et al. 1988.) In the deciding stage of attacks on aerial flocks, individual peregrines differed in method. They commonly maneuvered for position above the spherical flock until they stooped perpendicularly with rigid wings, either held open or tucked in. From a distance, it might seem as if some falcons plunged right through the massed Dunlins. This could never be verified. Instead, the falcon often skirted the outside edge of the flock. At the terminus of its stoop, the peregrine typically drew level and attacked the bottom end of the flock (Fig. 1a). Other peregrines

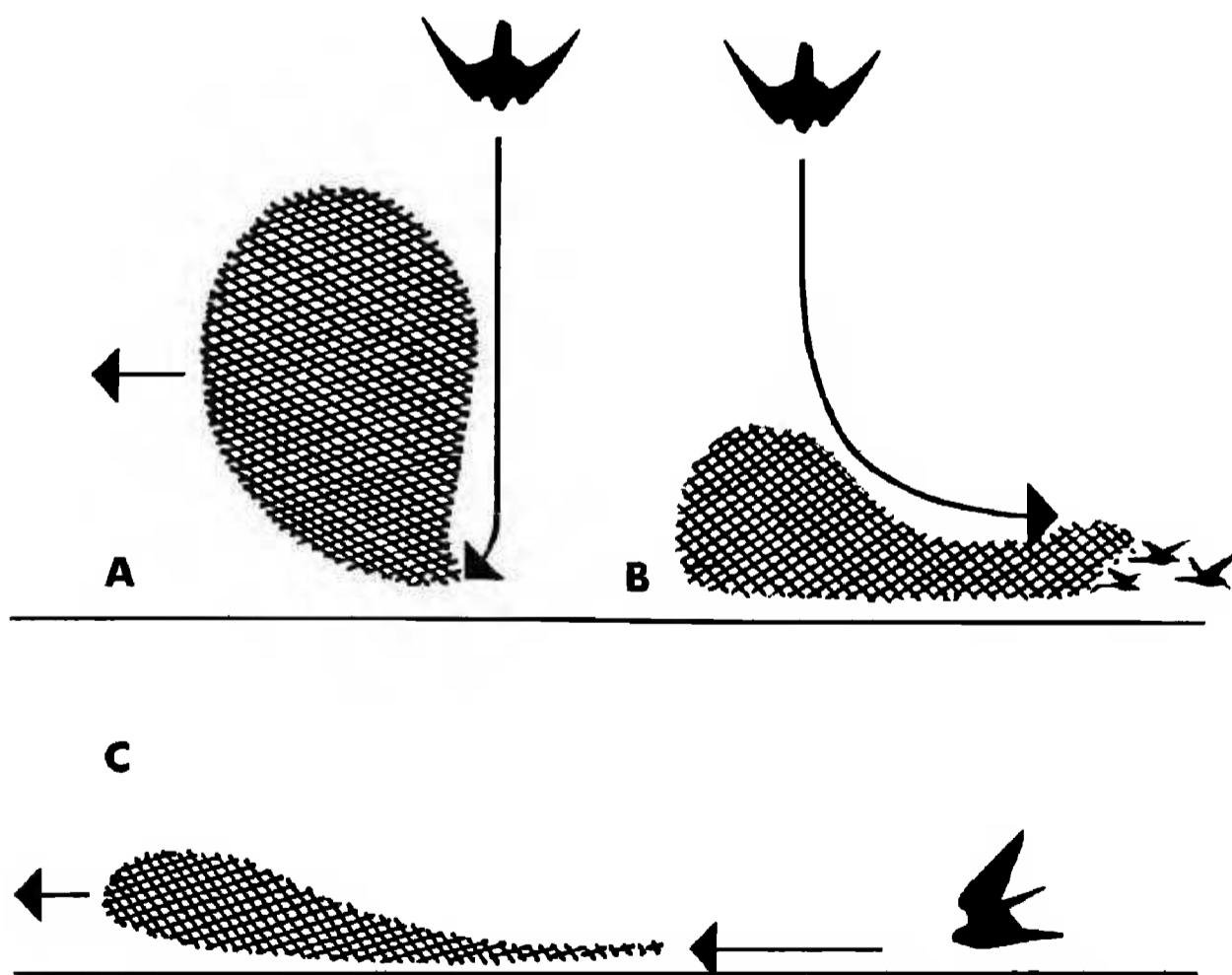


Figure 1. Strategies used by peregrines in attacks on flocks of Dunlins. The prey is either taken from the bottom, the edge, or the tail end of the flock. A. The peregrine stoops alongside of the flock and aims for the bottom. B. The peregrine stoops directly at the flock, which "caves in" and flattens out low over the water. C. Pursuit of flushing or low-flying flock.

stooped straight at the flock, which reacted by "caving in" and flattening out over the water while the falcon raked low over them (Fig. 1b). One or more Dunlins might splash down and take off again. Others may have been hit by the falcons. If the falcon failed to seize its prey at once, it either: (1) pursued a single Dunlin that split away from the flock; (2) regained altitude and maneuvered for another vertical stoop at the same flock; (3) attacked a different flock some distance away; or (4) ended the hunting sequence by perching or flying away.

In stealth hunts, when the peregrine approached in low flight (<1 m), flocks of Dunlins that flushed ahead might stay low as well, particularly during stormy weather when they commonly flew very low over the waves. If attacked and overtaken by a falcon, Dunlins in the trailing end of the low-flying flock could be seized (Fig. 1c). Single birds that dodged by dropping into the water and taking off again might be pursued and swooped at with varying degrees of persistence. Twenty-seven Dunlins were captured after individual pursuit including 3–10 passes. Two lone Dunlins, flying at 20–25 m, were seized by immature male peregrines that stooped nearly perpendicularly from a height of >100 m. In three separate, but unsuccessful instances, immature peregrines persisted in follow-chasing Dunlins >100 m high and far inland. After dodging 20–40 swoops, all three Dunlins descended and escaped into bushes.

The main hunting methods of stealth and open attack were used by all peregrines, although open attacks on flying flocks with multiple stoops appeared to be more typical of males than females. Immature males could be very persistent, but quite unsuccessful. For instance, on 21 January 2003, an immature male failed to make a capture over a period of 2.5 hr during which he launched three series of attacks over the low tide line, including a total of about 30 stoops at flocks. On 24 and 25 January 2003, an immature male made 22 and 33 consecutive stoops at flying flocks respectively, all without success. By contrast, on 11 November 2002, an adult male captured two Dunlins 20 min apart, each requiring only one stealth attack on roosting flocks. Of the total 652 hunts directed at Dunlins, 25% were made by adult peregrines, yet they accounted for 47% of the kills (Table 2). The success rate of adults was 26.8%, significantly higher than the 9.0% rate of immatures ($G = 19.92$, $P = <0.0001$).

Table 2. Success rates of Peregrine Falcons hunting Dunlins in British Columbia, and comparison with other studies of peregrines hunting shorebirds.

	HUNTS	KILLS	% SUC- CESS
This study (seacoast, winter)			
Adults	164	44	26.8
Immatures	399	36	9.0
Unidentified	89	14	15.7
Totals	652	94	14.4
Scotland ^a (seacoast, winter)	233	25	10.7
Alberta ^b (Prairie Lake, migration times)	569	50	7.2

^a Cresswell 1996.

^b Dekker 1988.

Unless they were hunting, adult males appeared to spend little time in the study area. On the other hand, adult females often perched for hours in the salt marsh or on inland cultivated land. On most days, two different adult females perched ca. 3 km apart. Evidently territorial, they attacked and chased off other females, either adult or immature. By contrast, the females tolerated males, and often joined them in attacking flocks of Dunlins. Frequently, both sexes pursued the same Dunlin, which might be captured by either one. However, if the male made the capture, he was chased and robbed by the female. Fourteen males dropped their prey, others were pursued far away and out of sight. Probably to avoid piracy by conspecifics, some male peregrines, upon capturing a Dunlin, flew to forested headlands across the bay. Four males circled to a high altitude and consumed their prey on the wing. The peregrines also robbed four Merlins (*Falco columbarius*) of their freshly-caught Dunlins. Peregrines hunted Dunlins throughout the day; 46 kills were made prior to 1200 H and 48 after 1200 H. The respective values for kills per hour of observation (1/8.1 and 1/12.4) were not significantly different ($G = 2.85$, $P > 0.05$). Peregrines often resumed hunting immediately after eating a Dunlin, which took 10–20 min.

Duck Hunts. The peregrines rarely hunted ducks in the study area. Only four kills were seen. A Green-winged Teal (*Anas crecca*), that was flushed and briefly pursued by an adult male, was seized in a shallow pool on the edge of the salt marsh.

The peregrine carried his prey out of sight low over the marsh. Female peregrines pursued and captured three ducks larger than teal, presumably Northern Pintails (*Anas acuta*), which were seized on the ground after the ducks dodged the approaching falcon by dropping onto the wet tide flats.

Kleptoparasites. All three large ducks captured by peregrines in the study area were forfeited without a fight to approaching Bald Eagles. Four other peregrines that chased and harassed ducks for some distance were shadowed by one or more Bald Eagles, which attempted to seize ducks that dodged the peregrine by ditching into the water. Eagles also commonly interfered with peregrines that were hunting Dunlins. At least 50 of 94 peregrines, which had just caught Dunlins, were immediately pursued by one or more eagles. The falcons usually managed to stay ahead of eagles. However, three peregrines, closely harassed by 2–4 eagles, released their Dunlins. Two of these falling prey items were retrieved in mid-air by one of the eagles. In at least three cases, eagles pounced on and captured Dunlins that had ditched into the water or dropped into grassy vegetation to dodge the falcon.

The following incident is a typical example of intra- and interspecific competition between falcons and eagles. In the afternoon of 16 January 2003, a male peregrine stooped at a flock of Dunlins and pursued a single bird that split off and dodged repeated passes. The male was quickly joined by a female peregrine and four eagles. All of these alternately swooped at, or tried to swoop at the Dunlin which flew erratically 1–10 m high over the water. After a combined total of 10–12 passes, the Dunlin was caught by the female peregrine, which was immediately set upon by the eagles. The peregrine managed to escape and carry her prey far inland. Prey-carrying peregrines were frequently, but vainly, chased by Glaucous-winged Gulls (*Larus glaucescens*). In addition, gulls often joined peregrines that were pursuing lone Dunlins, and on two occasions gulls pounced on Dunlins that had ditched into the water to escape a swooping peregrine.

DISCUSSION

The stealth tactics used by the falcons in this study were similar to those reported for migrating peregrines hunting shorebirds in central Alberta, although, due to more favorable weather condi-

tions, the migrant falcons launched their stealth attacks more often from high soaring flight (Dekker 1980, 1988, 1999). The percentage of stealth hunts in the two studies is, however, quite different (35% at Boundary Bay vs. 77% in Alberta). The explanation can be found in the difference in respective habitats. The Alberta falcons hunted over reed-studded shallows of a large inland lake, which afforded ample opportunities for a concealed approach. By contrast, the relatively low use of stealth on the coast of British Columbia reflects the lack of opportunity for effective surprise over the tide flats. The percentage of stealth hunts in this study is nearly equivalent to the 36% reported from the east coast of Scotland (Cresswell 1996).

It is possible that stealth hunts, especially successful ones by adult peregrines, are under-recorded in this study, resulting in a bias in favor of open hunts. Successful stealth attacks on flocks of Dunlins roosting near the salt marsh easily escape detection by the human observer. Stealth attacks are often initiated from distances of >1 km and the terminal portion takes place very low over the ground or water. The light-colored plumage of the adult falcon blends into the background of water and renders it more difficult to detect than a dark immature peregrine. Screened by the massive flushing of hundreds or thousands of Dunlins, the attacking peregrine might carry its prey away before the observer is aware of what happened. Adult falcons are competent in the use of stealth and especially the male tends to keep a low profile, perhaps to avoid attracting the attention of kleptoparasites.

In contrast to stealth attacks, open hunts are readily observed because the observer is alerted to the arrival of the predator by the rising of dense flocks of Dunlins. However, during a prolonged series of attacks, it is difficult to keep accurate score of the exact number of falcon hunts. Stoops on flocks can follow each other in rapid succession and the observer often cannot determine if a stoop was aimed at the same or a different flock. To avoid this problem, Buchanan et al. (1986) used the term hunting flight, which is defined as “a perch to perch flight involving one or more capture attempts.” Although the number of kills was very small ($N = 7$), Buchanan et al. (1986) calculated the success rate of hunting flights as 47% and that of individual capture attempts as 14.6%.

Any study of the hunting habits of the Peregrine Falcon involves a certain amount of subjective in-

terpretation, which might in part explain the variance between studies (White et al. 2002). In my appraisal of open hunts, I kept score of separate attacks in a conservative way, concentrating on the outcome. How the kill was made seemed of more importance than how often the falcon missed. Many hunts that fail may not be all that intense. This possibility was pointed out by Treleven (1980), who coined the terms high-intensity and low-intensity hunting.

Based on the examination of prey remains, a high proportion of shorebirds killed by raptors were reported to be juveniles (Whitfield 1985, War-nock 1994). Kus et al. (1984) suggested that this may be due to age-related differences in Dunlin flocking behavior. I postulate that the mechanics of prey selection may be very simple. Sixty-five (69%) of the Dunlins captured during this study were taken from the outside or the tail end of flocks (Fig. 1). Flocking is a well-known predator avoidance behavior of open-country birds. Their drawing together into dense aerial formations is the result of each bird's instinctive desire to find safety in the center of the flock (Tinbergen 1951). I speculate that adults are more proficient at this than juveniles, which are left on the outside of the flock. Several studies have reported age-related segregation of birds in roosting and feeding flocks (Newton 1998). If peregrines selectively remove juvenile Dunlins from a wintering population because they are easier to capture than adults, then the proportion of vulnerable juveniles in that population should decline over the course of the winter. Furthermore, juveniles that are attacked on a daily basis and manage to survive for several months, might learn to become more vigilant and avoid capture. These conclusions seem to be supported by the data. The respective hunting success rates of peregrines for November and January decline from 18.6% ($N = 134$) to 12.4% ($N = 404$), although the difference is not significant ($G = 2.30$, $P > 0.05$).

The kleptoparasitic habits of Bald Eagles are well known, particularly at the expense of peregrines that hunt ducks or seabirds (Anderson and DeBruyn 1979, Dekker 1995, Dekker and Bogaert 1997). Bald Eagles also kleptoparasitize Merlins. During this study, Merlins were seen to capture 14 Dunlins, two of which were pirated by pursuing eagles. Buchanan (1988) reported similar instances and he suggested that the threat of losing prey to a kleptoparasite resulted in Merlins engaging in

hunting flights of shorter duration when potential kleptoparasites were present. Gyrfalcons (*Falco rusticolus*) wintering in Alberta were often robbed of ducks by eagles as well and avoided hunting at localities where Bald Eagles sat on prominent perches (Dekker and Court 2003).

In conclusion, I suggest that the ubiquitous presence of eagles at Boundary Bay discourages wintering peregrines from hunting ducks on the tide flats. The possibility exists that peregrines may hunt ducks more often at night or at inland localities where eagle presence is lower than on the coast. Adult female peregrines, which had perched on the coast for much of the day, flew inland at dusk when ducks also leave the coast to feed on inland meadows (Dekker 1999). During November, when eagles are far less numerous at Boundary Bay than in January, several immature peregrines hunted ducks persistently in the study area. As the winter progresses however, I surmise that these juveniles eventually stop hunting ducks on the tide flats and instead concentrate on prey such as the Dunlin that can easily be transported over long distances, out of reach of kleptoparasitic eagles.

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